ECOLOGICAL SOCIETY OF AMERICA

Ecology/Ecological Monographs/Ecological Applications

PREPRINT

The doi for this manuscript and the correct format for citing the paper are given at the top of the online (html) abstract.

Once the final published version of this paper is posted online, it will replace the preliminary version at the specified doi.

Type of contribution: Article

Running Head: Food and space use of vultures

Food predictability determines space use of endangered vultures: implications for management of supplementary feeding

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Word count: 6015 (including abstract, main text and acknowledgements)

Abstract

Understanding space use of free-living endangered animals is key to inform management decisions for conservation planning. Like most scavengers, vultures have evolved under a context of unpredictability of food resources (i.e. exploiting scattered carcasses that are intermittently available). However, the role of predictable sources of food in shaping spatial ecology of vultures has seldom been studied in detail. Here, we quantify the home range of the Egyptian vulture (*Neophron percnopterus*), a long-lived raptor which has experienced severe population decline throughout its range and is qualified as endangered worldwide. To this end six adults were tracked by satellite telemetry in Spain during the breeding season, from 2007 to 2012, recording 10360 GPS locations. Using Resource Utilization Functions, we assessed the topology of the Utilization Distribution, a three-dimensional measure that shows the probability of finding an animal within the home range. Our results showed how food availability and principally, how food predictability, determines ranging behaviour of this species. Egyptian vultures showed consistent site fidelity across years, measured as the two and three-dimensional overlap in their home ranges. Space use varied considerably within the home range and remarkably, places located far from nesting sites were used more frequently than some areas located closer. Therefore, traditional conservation measures based on establishing restrictive rules within a fixed radius around nesting sites could be biologically meaningless if other areas within the home range are not protected too. Finally, our results emphasize the importance of anthropogenic predictable sources of food (mainly vulture restaurants) in shaping the space use of scavengers, which is in agreement with recent findings. Hence, measures aimed at ensuring food availability are essential to preserve this endangered vulture, especially in the present

context of limiting carrion dumping in the field due to sanitary regulations according to European legislation.

Key words: conservation; home range; kernel density estimators; resource utilization functions; satellite telemetry; spatial ecology; utilization distribution; vulture restaurants.

INTRODUCTION

Vultures have suffered a dramatic decline worldwide, particularly in Asia and Africa as a consequence of human direct persecution, indirect poisoning to kill carnivores and by the veterinary drug diclofenac (Ogada et al. 2012). In Europe, besides direct and indirect persecution, main threats include changes in livestock husbandry practices from traditional extensive grazing to an intensive industry, and especially, shortage of food supply as a consequence of European sanitary regulations due to an outbreak of bovine spongiform encephalopathy (BSE) in 2001 (Margalida et al. 2010). These caused changes in vultures' behaviour (Zuberogoitia et al. 2010, 2013), decreased breeding success and have increased mortality among younger age classes (review in Donázar et al. 2009, Martínez-Abraín et al. 2012).

Understanding space use of far-ranging animals, such as vultures, is crucial for conservation planning and, especially, to inform management decisions regarding endangered species (Bograd et al. 2010, Kertson and Marzluff 2011). The combination of recent advances in "biologging" technologies (i.e. the use of miniaturized animal-attached tags for studying animal's movements, behaviour, physiology and/or environment) with latest analytical techniques has allowed us to make a quantum leap in the field of movement ecology (Kernohan et al. 2001, Nathan et al. 2008, Rutz and Hays 2009). Paradoxically, despite the endangered status of most vulture species, our knowledge about ranging behaviour of scavengers is still very limited. Most of our current knowledge is based on the inference from field observations of marked animals, direct observations in particular areas (e.g. breeding territories, vulture restaurants and migratory bottlenecks) and limited spatio-temporal tracking using VHF telemetry (Donázar 1993, DeVault et al. 2004). However, there is little information from continued long-term remote tracking of

individuals by means of satellite telemetry (Meyburg et al. 2004, García-Ripollés et al. 2010, 2011, López-López et al. 2013, Monsarrat et al. 2013, Phipps et al. 2013).

Vultures are the only obligate vertebrate scavengers and have evolved under a context of unpredictability of food resources (i.e. exploiting scattered carcasses that are intermittently available) (Ruxton and Houston 2004). They provide irreplaceable ecosystem services such as waste removal, nutrient recycling and limit the risk of disease transmission (DeVault et al. 2003, Ogada et al. 2012). This, coupled with their rapid decline worldwide has led them to be qualified as priority species for conservation (Directive 2009/147/EC of the European Union on the Conservation of Wild Birds). The Egyptian vulture, *Neophron percnopterus*, could be one of the species potentially most affected by changes in cattle management regime, mainly owing to its low competitive ability against other vultures (Cortés-Avizanda et al. 2010) and its low population size (García-Ripollés and López-López 2011). Therefore, the quantification of space use and the relationship between environmental features and ranging behaviour is critical to achieve a better understanding of the spatial ecology of this scavenger. Moreover this will ultimately help to inform management actions for its conservation.

The main goals of this study were to: (i) evaluate and quantify Egyptian vultures' home range size during the breeding season; (ii) investigate the relationship between space use and external factors (i.e. environmental variables) across years and within the breeding season, with particular emphasis on how food availability, and especially, how anthropogenic predictable sources of food are determinants of space use and shape the home range; (iii) analyse the degree of repeatability (i.e. site fidelity) in the patterns of space use of individuals, both between years and within the breeding season; and finally (iv) derive management recommendations for

environmental assessments, for the management of anthropogenic food subsidies, and ultimately, for conservation plans of scavengers species.

METHODS

Study species

The Egyptian vulture is a long-lived medium-sized raptor which has experienced severe population decline throughout its range and is endangered worldwide according to the IUCN Red List (BirdLife International 2013). Reasons for this decline include disturbance at nesting sites, direct and indirect poisoning, electrocution by power lines and reduced food availability due to changes in traditional farming practices (BirdLife International 2013). Spain, where 1452 - 1556 pairs were surveyed in 2008, holds 30-45% of the European population (Del Moral 2009). Egyptian vultures feed mainly on carrion but occasionally take small vertebrates, eggs and even faeces (Ferguson-Lees and Christie 2001). They are territorial breeders, but roost communally on large trees and cliffs placed near suitable foraging areas, which include dump sites, vulture restaurants and livestock farms. The European continental populations are migratory and travel from their breeding grounds to wintering areas located in the Sahel region of Africa (Ferguson-Lees and Christie 2001, García-Ripollés et al. 2010).

Data Collection

To quantify Egyptian vultures' space use, we captured six adults at two vulture restaurants located in Castellón and Guadalajara provinces (Spain) and at ad-hoc artificial feeding stations located within breeding territories from 2007 to 2009 (Fig. 1). We used bownet traps baited with giblets to capture the birds. A 45 g solar-powered GPS tag from Microwave Telemetry Inc. was

mounted in a backpack configuration and attached using cotton ribbon, designed to ensure that the harness would fall off at the end of the tag's life. The mass of the equipment, including the harness, metal ring and tag, was below 3% of the bird's body mass, which is within recommended limits (Kenward 2001). The GPS tags were programmed to obtain GPS fixes every two hours during the breeding season (February-September) on a 16 hours ON/8 hours OFF duty cycle (06:00h – 22:00h, Greenwich Mean Time), which coincided with vulture activity during daylight hours. Data were retrieved and managed using the Satellite Tracking and Analysis Tool (Coyne and Godley 2005).

Only locations recorded during complete breeding seasons, i.e. since the arrival in Europe from the African wintering grounds (February-March) until the onset of autumn migration (August-September), were included in this study. Therefore, we discarded the data belonging to the breeding season in which birds were trapped. Data were filtered to exclude erroneous fixes (i.e. with 0 – 0 coordinates). Consecutive relocations at known roosting sites were included as only one independent fix to avoid a bias towards roosting areas in space use analyses (Seaman and Powell 1996, Kenward 2001). Nocturnal movements were also excluded since Egyptian vultures do not forage during the nighttime (López-López et al. 2013).

Field visits to each territory were also regularly conducted (three-five times per breeding season) to confirm the presence of the individuals, courtship, breeding behaviour, incubation and eventually, to record breeding success (further details about field methods are available in García-Ripollés and López-López 2006).

For the general goals of this study, data for each breeding season were divided into three periods: i) "pre-laying period", which spanned from the arrival at breeding areas until egg laying (March-April); ii) "incubation + nestling period", which comprised 42 days of incubation

(Ferguson Lees and Christie 2001) and the period in which nestlings remained in the nest just before their first flights (April to late July early August) (75 days on average; Donázar and Ceballos 1989); and iii) "pre-migration period", including the dependence period of juveniles until the onset of autumn migration to African wintering grounds (August-September). Egyptian vultures nest in caves so when birds began the incubation the GPS started to send irregular GPS locations and several 0-0 coordinates, a clear indication that the GPS was not directly exposed to sunlight. This circumstance, followed by an immediate field visit, allowed us to estimate the egg-laying date with an error of ± 3 days.

Space use

We quantified Egyptian vultures' home range by means of fixed-kernel density methods (Worton 1989, Kenward 2001). To assess different levels of space use, we computed 95%, 75% and 50% kernel density contours using the "Animal Movement" extension for ArcView 3.2 (Hooge and Eichenlaub 2000). The area encompassed within the 95% contour represents a standard measure of the home range, whereas the 50% kernel is usually considered a good indicator of the core area of activity (Seaman and Powell 1996; e.g. Campioni et al. 2013). We also included an intermediate measure (i.e. 75% kernel) to achieve a balance between the entire home range and the most used areas. We used the Least Squares Cross Validation method (LSCV) to calculate the smoothing parameter (Silverman 1986), which produces an objective and accurate estimate of home range size (Silverman 1986, Seaman and Powell 1996). The combination of kernel density estimators through location-based kernels and LSCV offers an optimal combination of ecological and statistical validity (Cumming and Cornélis 2012). Additionally, we also calculated the "overall" home range as the Minimum Convex Polygon

(MCP) encompassing all relocations obtained for each bird (Worton 1989). This estimate, although usually tends to overestimate the extent of the "true" home range (Seaman et al. 1999), was computed to facilitate comparisons with other studies and regions. Importantly, a preliminary analysis showed that there was no significant correlation between the four different measures of home range size (MCP, kernels 95%, 75% and 50%) and the number of relocations obtained per individual (Table B1, Appendix B). This preliminary test of the effect of sample size on the home range size is critical since it allows the ruling out of possible bias in the estimation of space use due to individual variability (Kernohan et al. 2001).

Spatial parameters

We calculated the average spider distance (SD) and the eccentricity (ECC) of home ranges, which both represent a measure of spread of the ranging area. SD is a linear indicator of the home range size and was calculated as the average distance from the arithmetic centre of all relocations (ACL) to each particular relocation (Hooge and Eichenlaub 2000). The eccentricity of home ranges was calculated as the distance from the nest used in each particular year to the ACL and was used to assess the extent to which the breeding area was centred on the home range (Bosch et al. 2010). Likewise measures of home range, spatial parameters did not correlate with the number of relocations per animal (Table B1, Appendix B).

Resource utilization functions analysis

Traditional resource selection analyses have been grounded in the comparison of resource use versus resource availability (Manly et al. 2002). Resource use can be easily quantified as the number of locations recorded in each resource class or as the proportional occurrence of a

resource within home range (Marzluff et al. 2004). However, obtaining an adequate measure of resource "availability" becomes a problematic question (Thomas and Taylor 1990, Millspaugh et al. 2006). To overcome this problem, Marzluff et al. (2004) proposed an alternative straightforward method based on relating resources to a probabilistic measure of space use, the so-called Utilization Distribution (UD). Basically, the UD is a probability density function obtained through kernel density analysis that shows the probability of finding an animal within the home range as a function of relocation points (Silverman 1986, Worton 1987, Kernohan et al. 2001). Therefore, we obtained the UDs for the combination of each individual-year (i.e. overall breeding season, N = 18; e.g. #75657-2009) as well as for each individual-period-year (N = 54; e.g. #75657-pre-laying-2009) using the "Animal Movement" extension for ArcView 3.2 (Hooge and Eichenlaub 2000). The UD displays a three-dimensional measure of space use across the home range in which the height of the UD represents the probability of use at each pixel (Millspaugh et al. 2006) (Fig. 1). Then, following Marzluff et al. (2004), we related space use with resource use using Resource Utilization Functions implemented in the "ruf" package (Handcock 2012) for R version 2.15.3 (R Core Team 2013). To that end, we sampled a set of environmental variables (i.e. resources) at each pixel of the UD and used multiple regression analysis to relate the UD height to these environmental predictor variables (Marzluff et al. 2004). Pixel size was determined by the smallest pixel size of the environmental variables (80 x 80 m), thereby increasing spatial resolution to the limit. The spatial extent of space use was defined as the 99% fixed kernel home range boundary (Marzluff et al. 2004, Kertson and Marzluff 2009). One of the main advantages of the RUF method is that it accounts for spatial autocorrelation by incorporating a Matern correlation function (Handcock and Stein 1993, Marzluff et al. 2004). The importance of each resource to variations in the UD (i.e. the measure of resource use) was

indicated by the magnitude of the standardized coefficients of the RUFs (Marzluff et al. 2004). A complete review of the basics and a discussion of the pros and cons of RUFs can be found in Marzluff et al. (2004), Millspaugh et al. (2006) and Hooten et al. (2013).

Environmental variables

To extract landscape metrics and relate them to the measures of space use we first created a sampling point grid that extended across the UD. This was done with the "Hawth Tools" extension (Beyer 2004) for ArcMap 9.2. (http://www.esri.com/). The UDs were firstly sampled to extract the values of space use (i.e. the height of the UD). Then, four sets of environmental variables were measured: topographic, land-use, population and food availability. We avoided sampling a large number of resources to prevent multicollinearity among predictor variables and include resources that could be biologically meaningless (Mac Nally 2000). Topographic variables included the measurement of the altitude of each pixel of the sampling grid through a digital elevation model (DEM) obtained from the Shuttle Radar Topography Mission with a resolution of 3-arc seconds (http://srtm.csi.cgiar.org/). We also calculated the aspect, which was derived from the DEM and was categorized into five main classes (1 = North; 2 = East; 3 = South; 4 = West; 5 = flat areas). The land cover layer was provided by the Corine 2000 Land Cover program (http://terrestrial.eionet.eu.int/CLC2000). Corine 2000 is divided into 44 land cover classes (i.e. third level CORINE codes). We grouped them into four main categories: artificial surfaces (ART = codes 111 - 142), agricultural areas (AGR = 211 - 244), forests and semi-natural areas (FOR = 311 - 335), and wetlands, water bodies and rivers (WAT = 411 - 523). The full Corine land cover legend is available through the European Environmental Agency web site (http://dataservice.eea.eu.int/dataservice/). Human population was obtained from the Spanish

Statistical Office (http://www.ine.es/) corresponding to the census conducted in 2011. Population density was computed in "Spatial Analyst tools" of ArcMap joining the population database with a point shapefile including the 8117 municipalities of Spain. Finally, eight resource levels of food availability were used in the analyses. Seven resources, including the number of horses, goats, sheep, cows, pigs, rabbits and poultry per municipality were obtained from the publicly available Agricultural Survey carried out in Spain in 2009 (http://www.ine.es/jaxi/menu.do?type=pcaxis&path=%2Ft01%2Fp042/E01&file=inebase&L=1). Finally, we incorporated an environmental variable including the presence/absence of predictable sources of food within the area encompassed by the full extension of all home ranges. This resource level included supplementary feeding places (i.e. vulture restaurants managed by the administration), dumping sites, plants of poultry waste treatment and cattle pens where cattle give birth their young. This layer was created and integrated into a raster dataset by combining information from different Spanish regional environmental administrations and specific fieldwork conducted throughout the study period. All samplings of resources were computed in Geospatial Modelling Environment software (Beyer 2012).

Site fidelity

To quantify site fidelity of individuals across years and between periods of the breeding season we calculated the two- and three-dimensional home range overlap (Kernohan et al. 2001) in ArcMap following Kertson and Marzluff (2009). Two-dimensional overlap provides a basic measure of site fidelity regardless of habitat use within the home range (Fieberg and Kochanny 2005). Furthermore, three-dimensional overlap takes into account differential probabilities of space use and quantifies site fidelity by means of the UD (Fieberg and Kochanny 2005). Further

249 details about specific formulae used for this analysis are available in Appendix A. In both cases,
250 site fidelity was tested at individual level (i.e. within-individuals). Between-individual overlap of
251 home ranges was not computed. Measures of two and three-dimensional overlap are given in
252 percentage ± standard deviation and range.
253
254 *Statistical analysis*
255 Space use and spatial parameters were analysed considering two temporal scales: i) an
256 "overall timescale" including each complete breeding season and ii) a "seasonal timescale"
257 divided into "pre-laying", "incubation + nestling" and "pre-migration" periods, separately (see
258 Campioni et al. 2003 for a similar approach). The former scale allowed us to provide a general
259 estimation of Egyptian vultures' spatial ecology and the latter scale to account for potential
260 variations in space use within the breeding period.
261 Firstly, we determined whether measures of home range size and spatial parameters were
262 normally distributed with the Shapiro-Wilk normality test. Since these variables did not follow a
263 normal distribution, descriptive results are given in median ± inter-quartile range (Gotelli and
264 Ellison 2004). Next, because we had repeated measures for the same individual between and
265 within years, we analysed overall and seasonal differences in home range size, spatial
266 parameters, standardized RUF coefficients and site fidelity by means of Linear Mixed Models
267 (LMMs) (Zuur et al. 2009). Differences between sexes were not tested due to limited sample
268 size. The variables "seasonal period" and "year" were included as fixed effects and the
269 "individual" was incorporated as a random effect. In order to find the best model structure, we
270 followed the top-down strategy suggested by Zuur et al. (2009). Initially, we fitted a full factorial
271 model ("beyond optimal model" *sensu* Zuur et al. 2009), then we tried different models, varying

the structure of fixed effects. These models were compared using the maximum likelihood estimation. Finally, having selected the best structure of fixed effects, we presented the best model using the restricted maximum likelihood estimation (Zuur et al. 2009). Models were validated by checking for homoscedasticity and normality of the residuals. To that end, relevant model diagnostic graphs were computed (residuals against fitted values, residuals against each explanatory variable, histogram of residuals and normality Q-Q plots) (Zuur et al. 2009). When required, variables were previously log-transformed to meet the assumptions of LMMs. For models including individual as the random term, we reported the intraclass correlation coefficient (ICC) which measures the correlation between observations from the same individual and can be interpreted as a measure of consistency of the results (Bartko 1966). It was computed as ICC = $d^2/(d^2 + \sigma^2)$, where d^2 is the covariance between any two observations for the same individual and its variance is $d^2 + \sigma^2$ (Zuur et al. 2009). Thus, higher ICC values indicate higher evenness among observations of the same individual. Moreover, we also reported a generalized R^2 for the random effect, calculated as the squared correlation between the fitted values of the model and the observed values of the data (Zheng and Agresti 2000). This value provides information about the amount of variation in the data explained by the random effect (i.e. between-individual variation) (Campioni et al. 2013). Computations were run with the "nlme" extension for R (Pinheiro et al. 2013).

We compared individual standardized RUF coefficients in order to rank resource use both at overall and seasonal scales. Relative importance of resources was evaluated by the magnitude (i.e. positive or negative sign) of the standardized RUF coefficients (Marzluff et al. 2004, Millspaugh et al. 2006). To test for consistency in selection of resource use at the population level we tested the null hypothesis that the average $\bar{\beta}$ was zero (see Marzluff et al. 2004 for a

complete description of this method). In addition, for the combination of each individual-period-year-resource category we ranked the models including topographic, land-use, population and food availability (including food predictability) resources by means of Akaike Information Criterion (Burnham and Anderson 2002). Statistical analyses were performed using STATISTICA version 10.0 (StatSoft Inc., www.statsoft.com). Statistical significance was set at $P < 0.05$.

RESULTS

Overall, 10360 valid GPS fixes were used for analyses, with an average of 1727 ± 856 relocations/bird (range = 643 – 2689). All birds were territorial breeders according to fieldwork. One bird (transmitter's code #75657) was tracked during five consecutive breeding seasons (2008-2012), three individuals (#80420, #89730 and #89731) were tracked during three breeding seasons (2010-2012) and two (#75659 and #80419) were tracked during two breeding seasons (2009-2010 and 2010-2011). According to molecular sexing, two birds were males (#80420 and #89731) and four birds were females (#75657, #75659, #80419 and #89730).

Home range size

Descriptive values of home range size and spatial parameters are available in Table 1. At the overall timescale, median size of home range areas ranged from 47 km^2 (core area), 101 km^2 (kernel 75%), 253 km^2 (kernel 95%) and 1257 km^2 (MCP). At this scale, home range size and spatial parameters did not show inter-annual variations (i.e. the variable "year" was not included in the best LMMs), thus showing evenness in ranging behaviour across years. At the seasonal timescale, home range size according to kernel 95%, kernel 75% and kernel 50% were

significantly lower during the "incubation + nestling" period (Fig. 2). The MCP size did not vary among periods. Moreover, we observed high intra-individual consistency in home range size (ICC_{MCP} = 0.36; ICC_{K95} = 0.42; ICC_{K75} = 0.36; ICC_{K50} = 0.29) and moderate levels of between-individual variation (R^2_{MCP} = 0.55; R^2_{K95} = 0.65; R^2_{K75} = 0.64; R^2_{K50} = 0.60).

Similar results were observed for spatial parameters. The measures of SD and ECC were significantly lower during the "incubation + nestling" period in comparison with the other two periods. Again, there was large intra-individual consistency in spatial parameters (ICC_{SD} = 0.39; ICC_{ECC} = 0.26) and intermediate levels of between-individual variation (R^2_{SD} = 0.51; R^2_{ECC} = 0.48). In all cases, validation results showed non-significant deviation of residuals from a normal distribution ($P > 0.05$ in all Shapiro-Wilk tests). Model validation graphs of LMMs are available in Appendix B (Figs. B1-B8). Remarkably, all birds' home ranges were eccentric both at overall and at seasonal timescales, indicating that breeding sites were not located in the centre of the home range (Table 1).

Predictors of space use

According to model ranking for the combination of each individual-period-year-resource category, the RUF analysis showed that the best predictors of space use at the individual level were those models including food variables, which were ranked first in 75.00% of cases. Models including population, topographic and land-use predictors were ranked first in 15.28%, 5.56% and 4.69% of cases, respectively (Fig. 3).

At the population level, the results of RUFs showed that Egyptian vultures showed increased space use in areas within the home range where food availability was higher, especially during the "incubation + nestling" period (Table 2). Particularly, in this period, Egyptian vultures

preferred areas with high density of sheep and poultry and avoided areas with high concentrations of horses, cows and pigs. During the "pre-laying" period, Egyptian vultures avoided areas of higher altitude and during the "incubation + nestling" period vultures decreased space use in southern-oriented areas. Importantly, the occurrence of predictable sources of food was the only predictor of space use that was positively selected in all three seasons (pre-laying: $P = 0.002$; incubation + nestling: $P = 0.002$; and pre-migration: $P = 0.014$; Table 2). These results showed high consistency at the population level, thus showing that food predictability plays a key role in shaping the UD for Egyptian vultures.

When standardized RUF coefficients were compared individually among seasons, results of LMMs showed that Egyptian vultures showed a clear preference for areas where predictable food resources and sheep density were higher (food predictability: model estimate ± standard error = 3.869 ± 1.652, $P = 0.019$; sheep: model estimate ± SE = 4.001 ± 1.652, $P = 0.016$). The other standardized RUF coefficients did not show differences at the seasonal timescale (Table B2, Appendix B). At the overall timescale, LMMs did not converge to a significant model, thus indicating that no relevant differences in measures of space use were detected across years.

Site fidelity

In relation to site fidelity, Egyptian vultures showed high level of two dimensional home range overlap at individual level across years and among periods of the breeding season. The percentage of overlap among seasonal periods was 68.02% ± 25.53% (range = 0.03 – 100, N = 126) and home range overlap within individuals across years was 72.76% ± 21.97% (range = 4.21 – 100; N = 42). No differences were observed in home range overlap either among seasonal periods or among years (all $P > 0.05$), mainly due to important intra-individual variation in home

range overlap (ICC_{SEASON} = 0.100; ICC_{YEAR} = 0.106) and low levels of between-individual variation (R^2_{SEASON} = 0.135; R^2_{YEAR} = 0.168).

Considering the UD, the percentage of three-dimensional overlap among periods was 55.13% ± 16.10 (range = 15.81 – 81.91, N = 63) and UD overlap across years was 67.72 ± 7.5 % (range = 45.19 – 76.54; N = 21). Significant differences were found in the degree of overlap at the seasonal timescale, which was higher during the "incubation + nestling" period (incubation + nestling: model estimate ± SE = 0.129 ± 0.048, P = 0.009). Between-individual variation in UD overlap was low (R^2_{SEASON} = 0.113). At the overall timescale, no differences were found in the degree of UD overlap across years. Intra-individual consistency in UD overlap was high (ICC_{YEAR} = 0.717) and between-individual variation was moderate (R^2_{YEAR} = 0.619).

DISCUSSION

The amount of information available about animal movement is increasing exponentially, allowing for rapid advances in our understanding of spatial ecology of organisms (Cooke et al. 2004). We are now able to answer old questions (i.e. when, where, and how far animals move during their life) with novel information, by quantifying animals' home range, obtaining probabilistic measures of space use and ultimately, linking them with resource selection (Silverman 1986, Worton 1989, Kernohan et al. 2001, Marzluff et al. 2004). To the best of our knowledge, here we showed the first quantitative assessment of the home range size of the Egyptian vulture by means of GPS satellite telemetry. Our results showed higher home range size, as calculated as MCPs or as according to fixed-kernel density estimators, than those reported in previous works. In fact, explicit works quantifying Egyptian vulture's home range were lacking and data which to compare our figures was usually immersed in other works about

other aspects of the basic ecology of Egyptian vultures. For example, home range size of a territorial adult tracked by radio-tracking in Spain was estimated in 21 km^2 (Ceballos and Donázar 1988) and between 10 km^2 and 15 km^2 in a similar study conducted in Israel with 10 pairs and two trios (Levy 1990). Donázar (1993) reported a core area size between 0.07 – 0.37 km^2. Home range size of two non-breeding adults ranged between 95 – 523 km^2 and was estimated of 40 km^2 for a non-breeding immature (Donázar 1993). Differences between our figures and those provided by previous studies are easily accounted for differences in the tracking methods, indicating that visual observation and radio-tracking tend to underestimate measures of home range size (Kenward 2001). Other authors estimated core area and home range size based on a circle with 1 km (3.14 km^2) and 8 km (≈ 200 km^2) radii from the nest respectively (Carrete et al. 2007), although these measures were set arbitrarily. The lack of accurate measures of Egyptian vulture's home range could be explained by the difficulty in capturing adult birds. Hitherto, the majority of Egyptian vultures marked have been nestlings which usually remain in the floater population, most of them in Africa (authors unpubl. data) until sexual maturity is attained, approximately at the age of five years (Grande et al. 2009).

Our results showed that home range size and spatial parameters did not vary across years, thus showing repeatability in ranging behaviour regardless of possible annual variations in ecological conditions. In contrast, home range was larger during the pre-laying and pre-migration periods than during the incubation + nestling period. All birds exhibited this common pattern regardless of individual variations in the absolute size of their home ranges. Spider distances showed that birds reduced their foraging movements during the period in which they were more linked to the nest, probably to defend their territory and to avoid predation of their chicks by other raptors (Newton 1979). Interestingly, our results showed that Egyptian vultures' home ranges were

410 eccentric, that is, territories were not centred in the nest site. This has important implications
411 both from an ecological and from a conservation point of view. Ecologically, the main
412 determinant of home range shape (i.e. according to kernels's topology) was the spatial
413 distribution of predictable sources of food. Similar results were found by Ceballos and Donázar
414 (1988), who found that maximum distances travelled by a marked individual was determined by
415 how far from its nesting site vulture restaurants were. Similar results have also been reported for
416 the Eurasian griffon vulture (*Gyps fulvus*) (García-Ripollés et al. 2011, Monsarrat et al. 2013).
417 Remarkably, our results showed that, for all birds, places far from nesting sites (i.e. between 20-
418 30 km) were used more frequently (i.e. higher UD values) than some areas closer (e.g. < 5 km).
419 This challenges common approaches in conservation that are based on the assessments of
420 potential threats within a pre-fixed radius around nesting sites, which is set arbitrarily by
421 researchers or by environmental authorities (Jennrich and Turner 1969). In fact, large-scale
422 conservation assessments, analyses of habitat preferences, demographic analyses and evaluations
423 of extinction risk were based on this approach, although in most cases they lacked biological
424 justification (e.g. Carrete et al. 2007, 2009, Grande et al. 2009). Therefore, although the
425 "precautionary principle" could be argued for this practice (thereby at least part of the core area
426 of activity is included), we urge that environmental risk assessments, conservation planning and
427 studies of resource selection should incorporate spatially explicit information and should be
428 evaluated case by case taking into account ranging behaviour of the target species rather than
429 relying on fixed radius around nesting sites which may miss additional areas of importance
430 within the home range.

431 According to the RUF analysis, the best predictors of Egyptian vulture space use at the
432 individual level were the availability of food resources. This result was consistent both across

433 years and within seasonal periods, with all individuals showing a similar pattern. Interestingly, at
434 the population level, our results emphasized the importance of predictable sources of food in
435 shaping the space use of this scavenger. Predictable sources of food included mainly vulture
436 restaurants and, to a lesser degree, other places such as traditional dump sites, slaughterhouses,
437 plants of poultry waste treatment and cattle pens where cattle is temporarily housed and give
438 birth their offspring. In fact, Egyptian vultures made long displacements daily or every two-three
439 days to these places (in some cases up to 250 km outward-and-return) where they could easily
440 fulfil feeding requirements. In the light of the on-going debate about the advantages and
441 shortcomings of supplementary feeding for vultures (Deygout et al. 2009, Donázar et al. 2009,
442 Cortés-Avizanda et al. 2010, Dupont et al. 2012), our results highlight the importance of
443 predictable sources of food in the trophic ecology and consequently, in the preservation of this
444 endangered scavenger. In addition, it also has an important conservation implication since
445 predictable sources of food are potential predictors of space use of scavengers (García-Ripollés
446 et al. 2011, Monsarrat et al. 2013, Phipps et al. 2013). Therefore, managers could take advantage
447 of this information and anticipate potential impacts of the construction of man-made structures
448 (e.g. wind-farms, power lines, etc.) close to or in the way to these predictable sources of food.
449 Conversely, managers can plan in advance the best location for vulture restaurants.

450 The magnitude of resource use by Egyptian vultures varied between seasonal periods.
451 Vultures increased space use in areas where food predictability was higher especially during the
452 pre-laying and pre-migration periods, likely to fulfil energy requirements after and before
453 migration (García-Ripollés et al. 2010, López-López et al. 2013). Egyptian vultures are territorial
454 breeders, but show an important social behaviour at these predictable sources of food, roosting
455 communally in the nearby (Cortés-Avizanda et al. 2011). According to our fieldwork, in all cases

456 communal roosting places were associated with predictable sources of food, particularly vulture
457 restaurants. Communal roosting places play a key role in pair bond, allowing the establishment
458 of social relationships and as information centres, where Egyptian vultures could take advantage
459 of a crowding effect (Cortés-Avizanda et al. 2011).
460
461 *Conservation implications*
462 Egyptian vultures showed high levels of site fidelity both according to two- and three-
463 dimensional overlap in their home range across years and among periods of the breeding season.
464 High degree of repeatability in space use indicates that ranging behaviour does not change
465 significantly over time, a similar pattern that has also been reported for other raptors (Campioni
466 et al. 2013). This is positive from the conservation point of view because it allows for the
467 establishment of effective long-term conservation measures if ecological conditions are not to
468 change.
469 Like most scavengers, Egyptian vultures are human-subsidized species nowadays, particularly
470 in Europe (Deygout et al. 2009, Oro et al. 2013). Vulture restaurants are an essential
471 conservation technique to preserve populations of endangered scavengers, always under
472 adequate sanitary guarantees and with a controlled carrion disposal (Dupont et al. 2012). From
473 an academic point of view, it is easily arguable that supplementary feeding management should
474 mimic natural conditions, based on numerous “light” feeding stations supplemented with low
475 quantities of food, thus simulating low predictability in food resources as it occurs in natural
476 conditions (Cortés-Avizanda et al. 2010, 2012, Monsarrat et al. 2013). Policies to favour
477 population recovery of wild herbivores and the authorization of the abandonment of livestock
478 carcasses in the field can also be advocated to help to maintain populations of avian scavengers

(Margalida et al. 2010). Notwithstanding, we consider that taking into account the current framework of highly subsidized cattle raising in Europe, especially by the Common Agricultural Policy of the European Union (http://europa.eu/pol/agr/index_en.htm), the lack of generational turnover in cattle farmers and the continuous process of abandonment of traditional pastoralism (Bernués et al. 2011), conservation planning of endangered species should meet reality and be more pragmatic. Recent findings have shown that predictable anthropogenic food subsidies may help to increase population numbers of endangered species through reduction in the variance of demographic parameters (Oro et al. 2013). Predictable sources of food buffer the influence of environmental stochasticity (Cortés-Avizanda et al. 2012, López-López et al. 2013) thus increasing the extinction time (Oro et al. 2013). Considering the key role of vulture restaurants in space use of Egyptian vultures, we advocate to keep them functioning to facilitate Egyptian vulture's population to increase at least to a better conservation status.

ACKNOWLEDGMENTS

We would like to thank L. Bolonio, J. De Lucas, V. García, R. Ibáñez, M. Nieto and Á. Vela for their help during field work. J. Marzluff, J. Zabala and L.M. Carrascal gave important methodological and statistical advice. P. López-López is supported by a "Juan de la Cierva" postdoctoral grant of the Spanish Ministry of Economy and Competitiveness (reference JCI-2011-09588). The authors declare that they have no conflict of interest. This paper complies with the current laws in Spain.

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685

SUPPLEMENTAL MATERIAL

Appendix A

Computation of two- and three-dimensional overlap in home ranges.

Appendix B

Correlation test between measures of home range size, spatial parameters and the number of relocations obtained per individual; LMM for the standardized RUF coefficients; and model validation graphs for the LMMs of the home range area.

694 TABLE 1. Home range size and spatial parameters of six adult Egyptian vultures tracked by GPS satellite telemetry in Spain.

695 Abbreviations: IQR = inter-quartile range; MCP = Minimum Convex Polygon; K = Fixed Kernel Density; SD = spider distance; ECC

696 = eccentricity. Surface units (i.e. MCP and kernels) are expressed in km^2 and distance units (SD and ECC) in meters. N = 18 in all

697 cases (i.e. six individuals per three periods and 18 breeding seasons overall).

	Period							
	Pre-laying		**Incubation + Nestling**		**Pre-migration**		**Overall breeding season**	
	Median	**(IQR)**	**Median**	**IQR**	**Median**	**IQR**	**Median**	**IQR**
MCP	272.9	(170.6 – 1701.8)	582.6	(435.9 – 741.7)	526.4	(370.0 – 1997.3)	1257.0	(745.2 – 3954.4)
K95%	262.5	(205.1 – 2313.8)	210.7	(125.4 – 254.8)	303.9	(131.3 – 2708.3)	253.3	(201.7 – 1669.9)
K75%	143.6	(75.0 – 1171.5)	51.4	(22.3 – 83.3)	76.3	(47.2 – 1037.0)	101.2	(62.9 – 660.6)
K50%	72.8	(43.2 – 649.9)	15.9	(11.9 – 33.5)	37.4	(26.3 – 555.5)	46.6	(26.4 – 343.7)
SD	13489.9	(8723.4 – 45118.2)	8219.8	(7037.8 – 14038.9)	11144.4	(8512.7 – 36675.9)	15453.6	(12098.2 – 30980.1)
ECC	17435.2	(7177.5 – 26750.3)	4828.0	(3471.4 – 9420.2)	7499.2	(4810.4 – 20795.2)	10400.8	(7627.3 – 14731.0)

698

699 TABLE 2. Estimates of standardized RUF coefficients (β) for six adult Egyptian vultures tracked by GPS satellite telemetry in Spain.
700 Significant results are highlighted with an asterisk. Abbreviations: ALT = altitude; ASP = aspect; AGR = agricultural areas; FOR =
701 forests and semi-natural areas; POP = human population density; HOR = horses; RABB = rabbits; POUL = poultry; PRED =
702 predictable sources of food.

		Period							
		Pre-laying				Incubation + Nestling			
Model	**Resource**	**Mean std. β**	**95% LCI**	**95% UCI**	**P(β =0)**	**Mean std. β**	**95% LCI**	**95% UCI**	**P(β =0)**
topographic		-0.318	-0.609	-0.027	0.033*	-0.302	-0.585	-0.019	0.037*
	ALT	-1.207	-2.290	-0.124	0.031*	-0.777	-1.907	0.353	0.165
	ASP1	-0.063	-0.230	0.104	0.436	-0.246	-0.515	0.023	0.071
	ASP2	-0.054	-0.275	0.167	0.613	-0.076	-0.316	0.164	0.513
	ASP3	0.053	-0.178	0.284	0.632	-0.109	-0.210	-0.008	0.036*
land-use		-1.971	-3.904	-0.037	0.046*	-0.721	-1.778	0.335	0.174
	AGR	-1.760	-4.148	0.628	0.137	-0.696	-2.086	0.693	0.302
	FOR	-2.182	-5.521	1.157	0.184	-0.746	-2.509	1.016	0.381
population	POP	1.038	-1.270	3.347	0.356	0.315	-1.270	1.901	0.680
food		-0.160	-2.501	2.180	0.892	-0.189	-1.367	0.989	0.752

HOR	-3.661	-8.351	1.029	0.118	-2.005	-3.686	-0.324	0.022*
GOAT	-9.168	-19.409	1.072	0.076	-3.487	-8.580	1.605	0.167
SHEEP	5.998	-2.870	14.866	0.172	3.272	0.117	6.428	0.043*
COWS	-5.566	-12.074	0.941	0.089	-4.527	-8.641	-0.414	0.033*
PIGS	1.176	-2.867	5.219	0.547	-1.915	-3.798	-0.032	0.047*
RABB	3.937	-4.163	12.037	0.320	0.516	-3.485	4.516	0.789
POULT	1.705	-3.872	7.283	0.527	3.370	0.445	6.294	0.026*
PRED	4.296	1.844	6.749	0.002*	3.265	1.372	5.158	0.002*

703

704

705 TABLE 2 (CONT)

		Period							
		Pre-migration				Overall breeding season			
Model	**Resource**	**Mean std. β**	**95% LCI**	**95% UCI**	**P(β =0)**	**Mean std. β**	**95% LCI**	**95% UCI**	**P(β =0)**
topographic		0.034	-0.291	0.360	0.835	-0.070	-0.191	0.050	0.247
	ALT	0.183	-1.179	1.545	0.780	-0.240	-0.746	0.265	0.330
	ASP1	0.023	-0.085	0.130	0.662	0.013	-0.033	0.058	0.564
	ASP2	0.013	-0.147	0.174	0.862	-0.024	-0.052	0.004	0.090
	ASP3	-0.083	-0.363	0.197	0.541	-0.030	-0.076	0.016	0.185
land-use		0.083	-0.721	0.888	0.835	-0.679	-1.623	0.265	0.153
	AGR	-0.184	-1.195	0.828	0.706	-0.606	-1.867	0.655	0.322
	FOR	0.350	-1.005	1.705	0.592	-0.752	-2.312	0.807	0.320
population	POP	-0.047	-0.774	0.681	0.893	0.406	-0.523	1.335	0.369
food		-0.192	-2.102	1.717	0.842	0.082	-0.662	0.826	0.828
	HOR	-0.094	-2.738	2.549	0.941	0.205	-0.182	0.592	0.279
	GOAT	3.729	-6.380	13.838	0.447	-2.528	-6.429	1.372	0.189
	SHEEP	0.135	-2.980	3.250	0.928	0.601	-0.775	1.976	0.370
	COWS	-2.209	-7.672	3.254	0.405	-1.434	-4.306	1.438	0.307

PIGS	1.304	-1.666	4.275	0.367	0.066	-0.617	0.749	0.840
RABB	-5.312	-14.791	4.167	0.253	1.966	-0.702	4.634	0.138
POULT	-0.541	-4.732	3.649	0.788	0.998	-1.157	3.153	0.342
PRED	1.449	0.327	2.571	0.014*	0.780	-0.215	1.775	0.116

706 Notes: Relative importance of resources is indicated by the magnitude (positive or negative) of mean standardized β (Marzluff et al.

707 2004). Consistency in selection at the population level is indicated by significance of β.

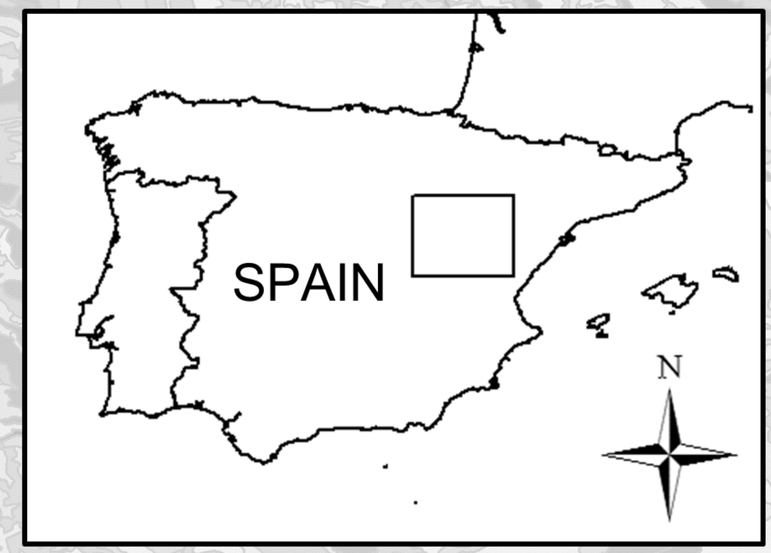
708 *P* values test the null hypothesis that the average β is zero (see Marzluff et al. 2004 for details).

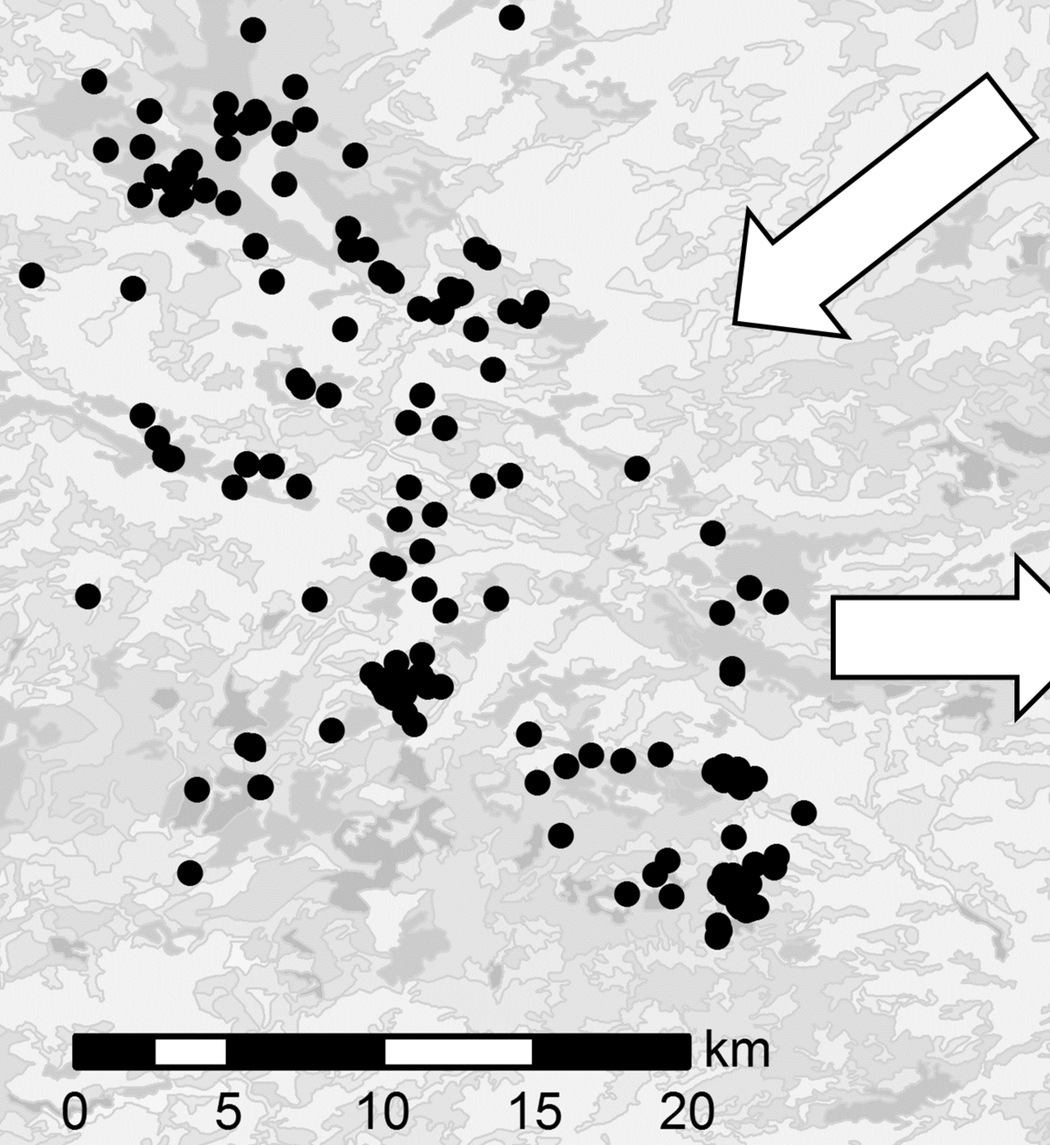
FIGURE CAPTIONS

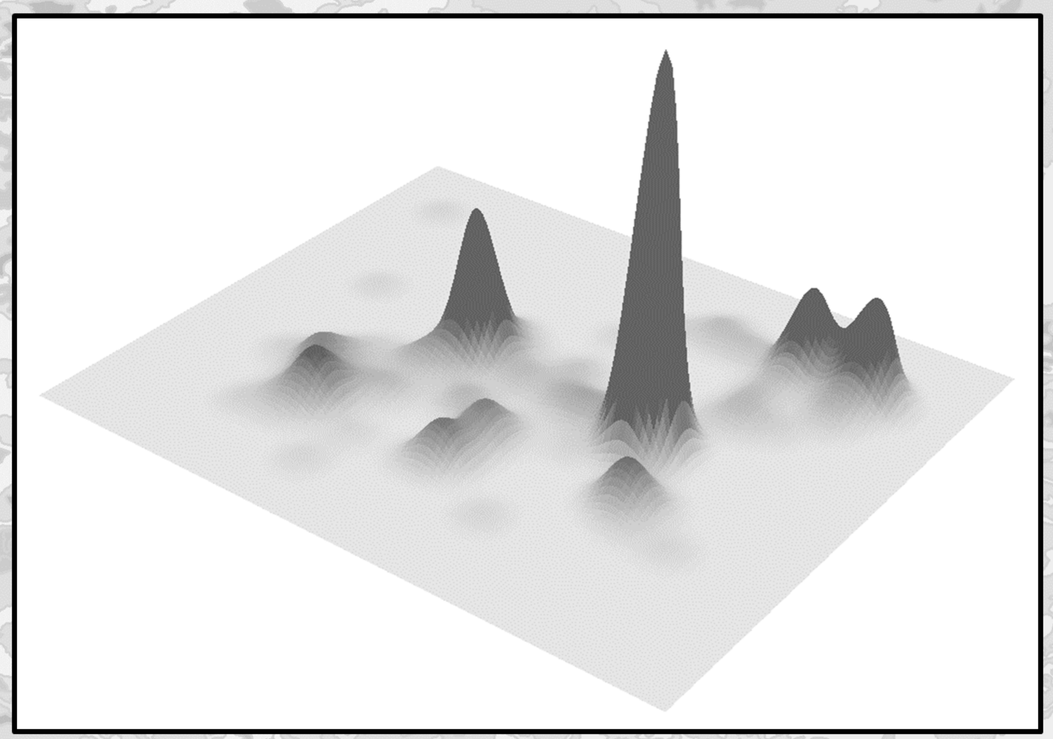
FIGURE 1. Study area within the Iberian Peninsula (upper left rectangle) and flow chart of the methods used in this study. Satellite fixes (lower left) were recorded for each Egyptian vulture tracked by GPS satellite telemetry (upper right) and were used for computing home range size, spatial parameters and their corresponding three-dimensional Utilization Distribution (UD, lower right). The height of the UD indicates the relative probability of use within the home range (Marzluff et al. 2004). Resource attributes (i.e. topographic, land-use, population and food availability) were sampled on a cell-by-cell basis from resource maps within the UD (e.g. in this case Corine land cover). These attributes were related to the height of the UD by means of multiple regression analysis adjusted for spatial autocorrelation, thereby obtaining the Resource Utilization Function (RUF) (Marzluff et al. 2004, see methods for details). Locations and UD shown here are illustrative of a particular example.

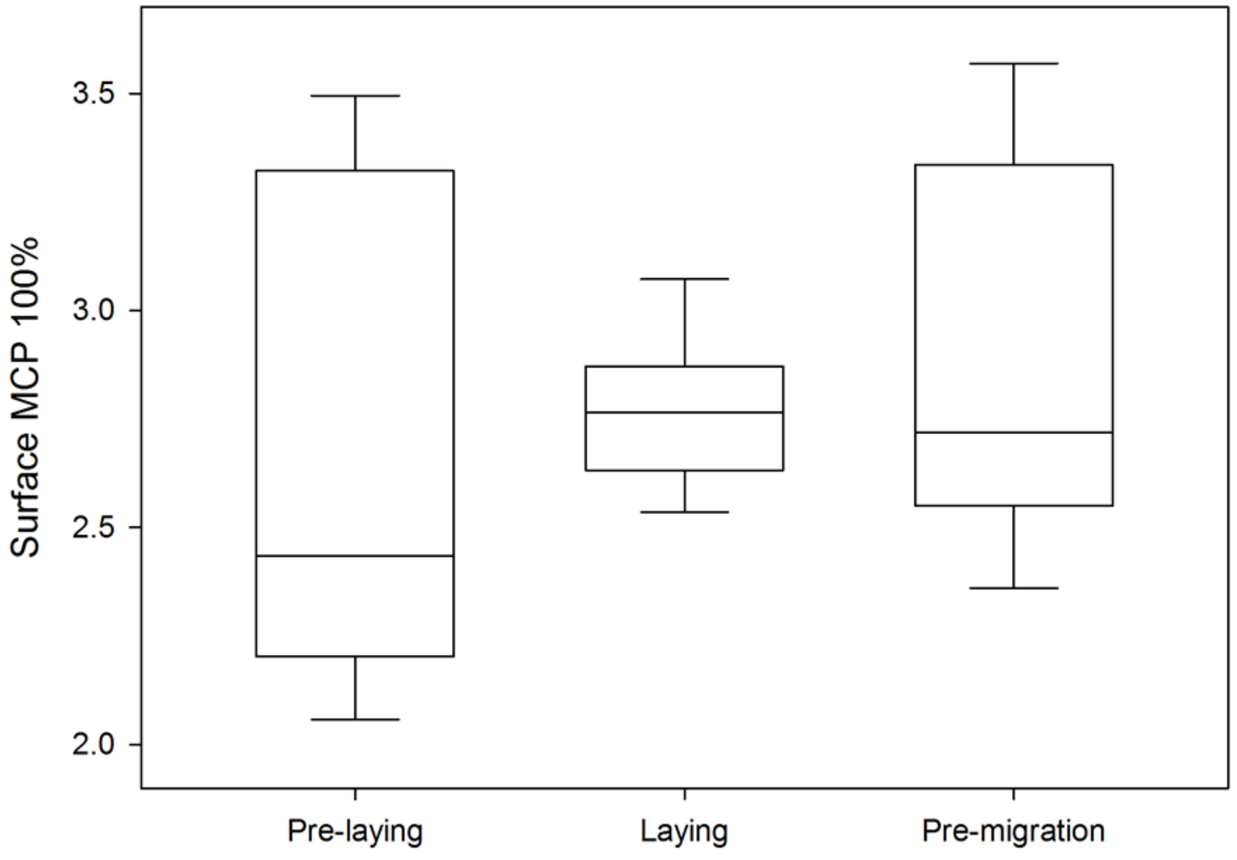
FIGURE 2. Boxplot of log-transformed home range size of adult Egyptian vultures satellite-tracked in Spain. Horizontal lines show the median and percentiles 5%, 25%, 75% and 95%. Home range size was significantly lower during the "incubation+nestling" period (excepting MCP) (see text for details).

FIGURE 3. Model rankings for each resource category according to Akaike Information Criterion. Differences in AIC (i.e. ΔAIC) were computed for the combination of each individual- period-year-resource category (N = 288 models). For example, models including the resource category "food" were ranked first in 75% of cases, 4% of cases in second place, 13% in third place and 8% in fourth place.


SPAIN
N


0
5
10
15
20
km

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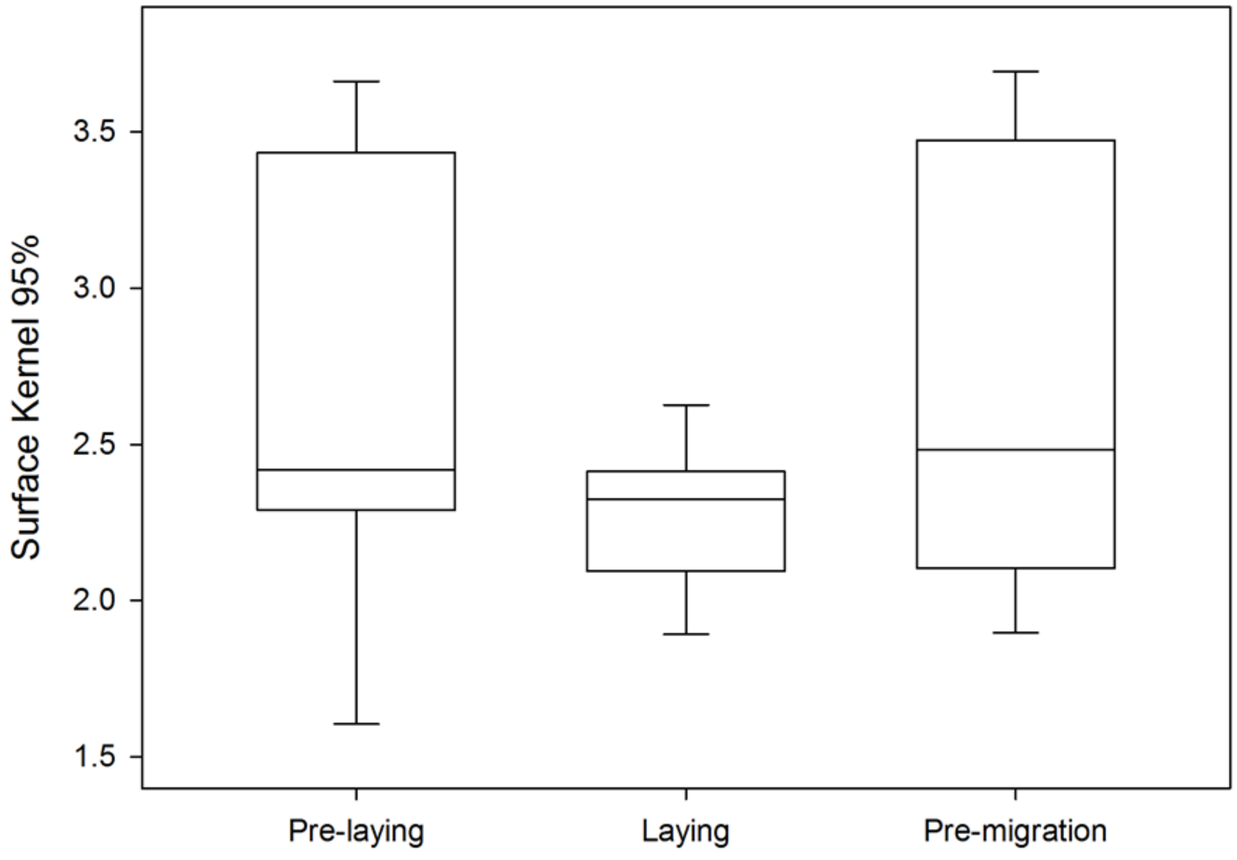
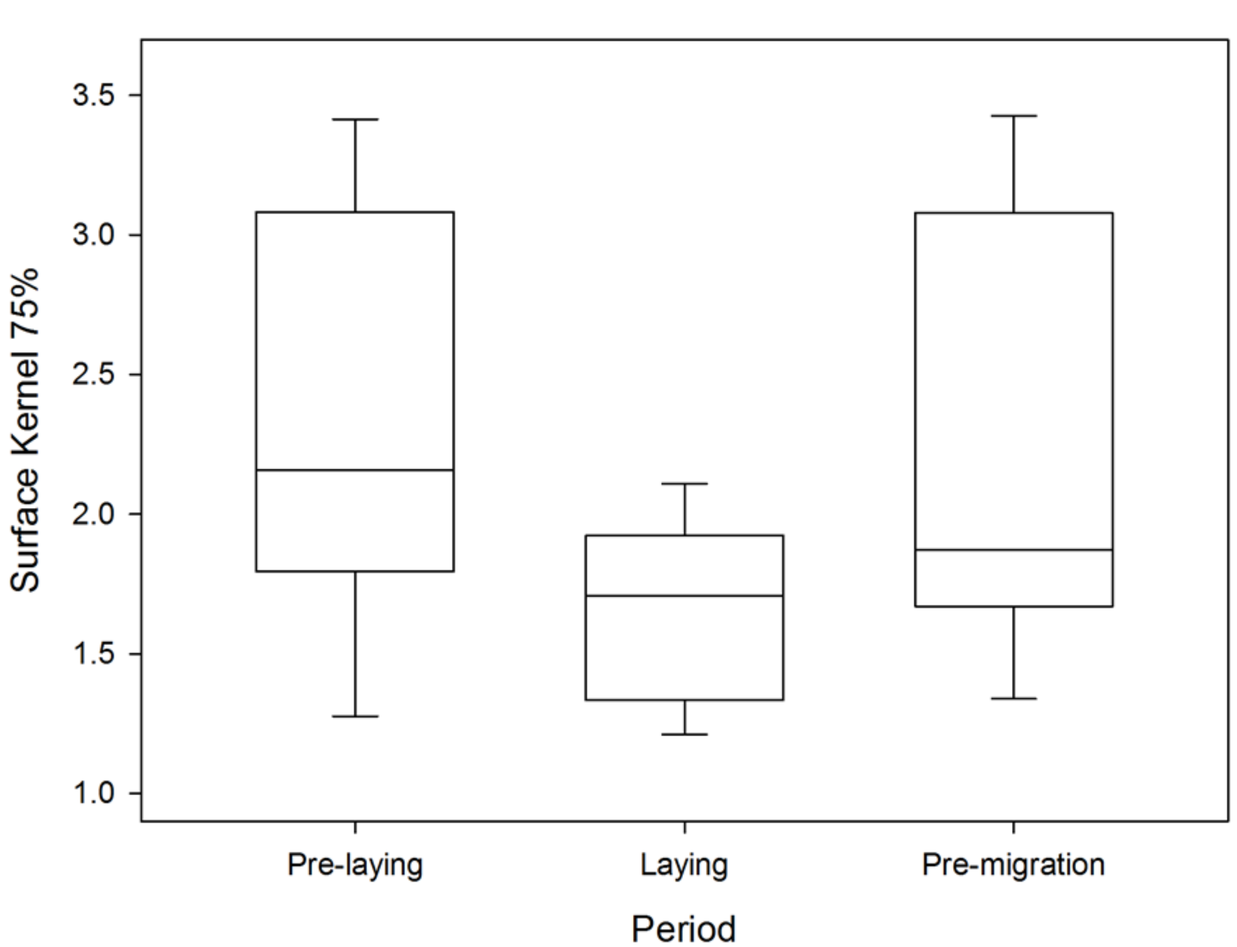
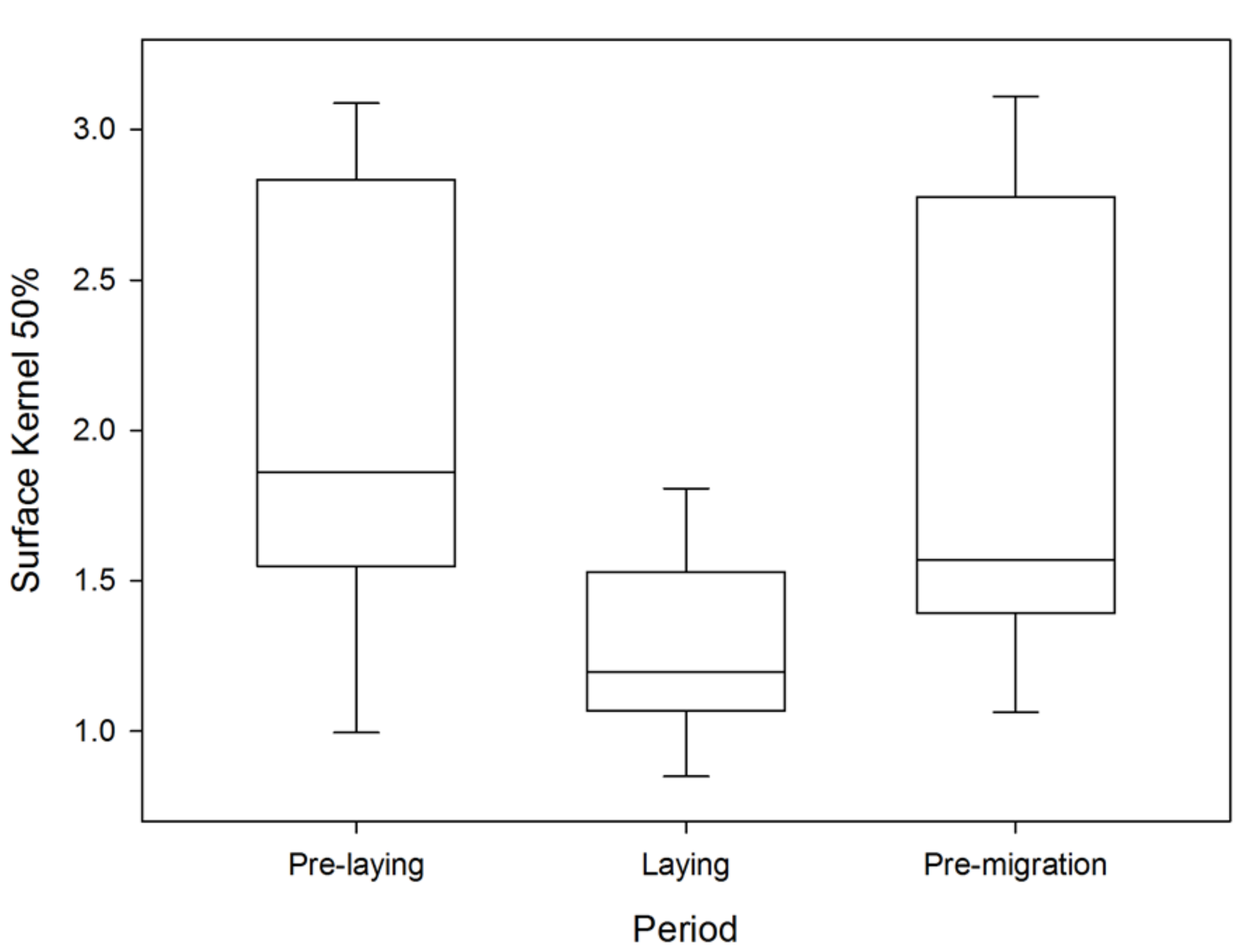
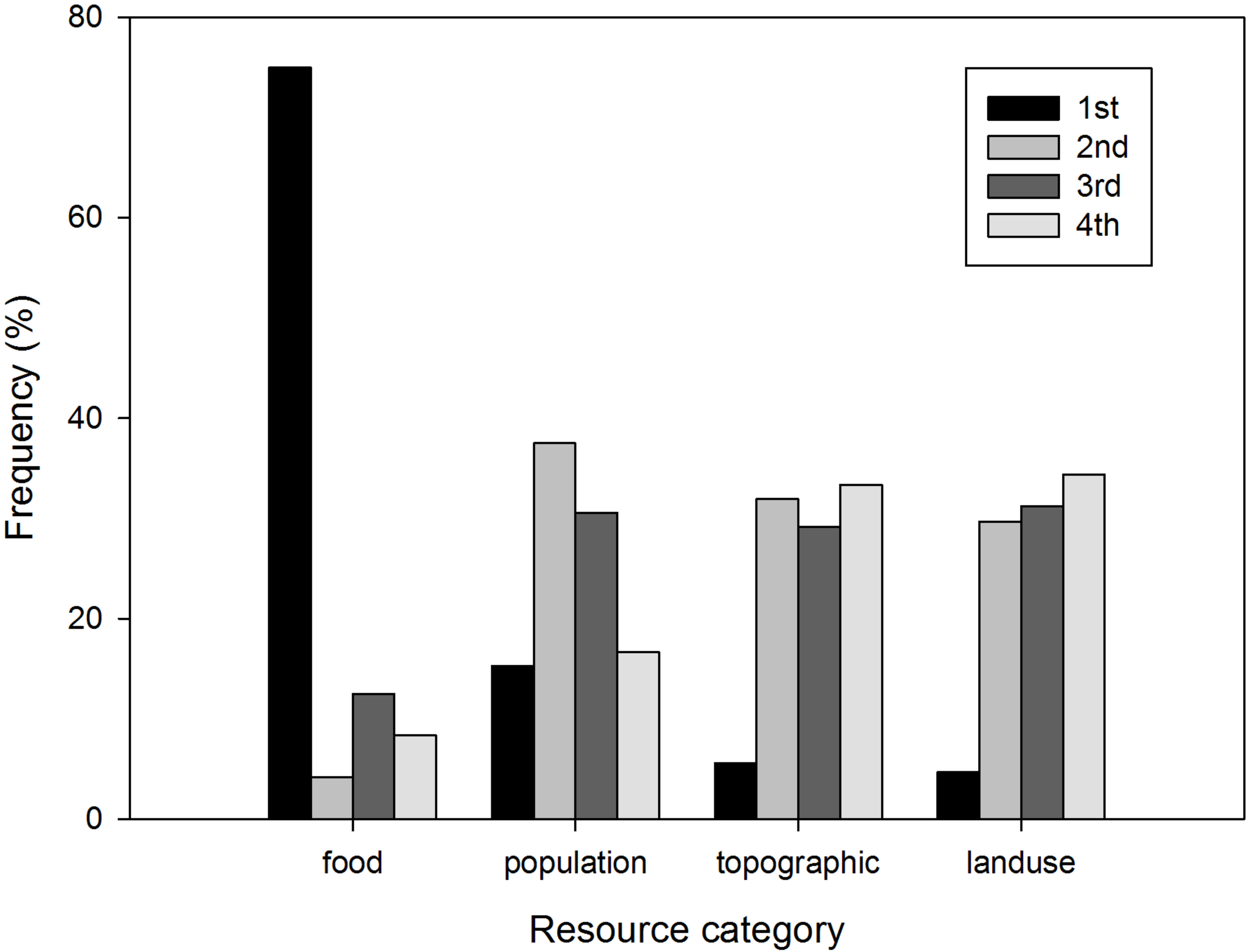
3.0
2.5
2.0
Pre-laying
Laying
Pre-migration


Surface Kernel 95%
3.5
3.0
2.5
2.0
1.5
Pre-laying
Laying
Pre-migration


Surface Kernel 75%
3.5
3.0
2.5
2.0
1.5
1.0
Pre-laying
Laying
Pre-migration
Period


Surface Kernel 50%
3.0
2.5
2.0
1.5
1.0
Pre-laying
Laying
Pre-migration
Period


80
60
40
20
0
Frequency (%)
1st
2nd
3rd
4th
food
population
topographic
landuse
Resource category